NEW ARCHAEOLOGICAL EVIDENCE ON EVOLUTION IN MAIZE

BY

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THE problem of the origin of maize, which for several generations past has commanded the attention of botanists and archaeologists alike, is appreciably nearer the point of final solution as a result of the discovery of important prehistoric plant remains in New Mexico during the summer of 1948. An expedition sponsored by the Peabody Museum of Harvard University[1] and led by Mr. Herbert W. Dick, a graduate student in anthropology, uncovered many cobs and other parts of maize from the accumulated refuse in an abandoned rock shelter, known as Bat Cave. This material not only furnishes direct proof of the nature of primitive maize but also provides for the first time tangible evidence of a well-defined evolutionary sequence in this important American cereal.

Anticipating the evidence to be presented in detail later in this paper, it can be said here that direct archaeological evidence is now available to show: (1) that primitive maize was both a pod corn and a pop corn; (2) that

[1] This expedition, the Early Man Division of the Upper Gila Expedition of the Peabody Museum of Harvard University, is under the general direction of Dr. J. O. Brew and is financed in part by the Viking Fund of New York City; the excavation of Bat Cave was in cooperation with the University of New Mexico. The general aims of the Expedition are set forth by Brew and Danson (1948).

maize did not originate from teosinte; (3) that much of the variation in modern maize is the product of introgression from teosinte which occurred as a later step in the evolution of maize.

The prehistoric maize remains which permit us to draw these far-reaching conclusions comprise a considerable part of the total vegetal remains isolated from the refuse in Bat Cave by Mr. C. Earle Smith, Jr., the junior author of this paper, who served as botanist to the expedition. The vegetal remains other than maize, which are also of considerable ethnobotanical interest, will be described separately by Mr. Smith. Suffice it to say here that, in addition to maize, seeds of both kidney beans and squashes were found at all except the lowest levels of the Bat Cave refuse in which maize itself occurs.

DESCRIPTION OF BAT CAVE

Location and Climate. Bat Cave is located in Catron County, New Mexico, on the edge of the Plains of San Augustin, the basin of an ancient lake of considerable size which has been described by Powers (1939). The longitudinal axis of the basin which lies in a northeast to southwest direction is about 60 miles. The basin varies from six to twenty miles in width.

There are no natural streams permanently flowing into the basin and the plains are dry for the better part of the year. The arroyos and canyons carry water only during the rainy season in July and August, when afternoon showers sometimes precipitate large amounts of water in a short period of time. Records kept at Aragon, a village about 25 miles from the site, indicate an average annual rainfall of approximately 14 inches; the precipitation, at present, on the plains of San Augustin, is probably a few inches less.

Present Vegetation. The paucity of water in the re-

gion greatly restricts the natural vegetation. In the immediate vicinity of the site at Bat Cave *Atriplex canescens* (Pursh) Nutt. provides the major cover on the plain with species of Sporobolus and Heliotropium playing a secondary rôle. There is a distinct change in the vegetation as one leaves the old lake floor and ascends the gravelly beach terraces which mark the ancient shores of the lake. Russian thistle, *Salsola pestifer* A. Nels., is common on the edge of the plain. Many species of Compositae, Labiatae, Chenopodiaceae, Amaranthaceae, Boraginaceae and Gramineae are found on the terraces themselves. Where the terraces are especially rocky, *Fallugia paradoxa* (D. Don) Endl. occurs as a common shrub with *Rhus trilobata* Nutt. ex Torr. & Gray and species of Ribes and Forsteria. During the dry season this vegetation has a distinctly xerophytic appearance accented by occasional plants of Opuntia and Mammillaria. In the rainy season the vegetation becomes quite green, and a number of short-lived annual flowering plants, as well as species of Selaginella and Notholaena, make their appearance.

The vegetation remains more or less the same for some 200 to 400 feet up the slopes surrounding the basin. At this point a distinct change in the vegetational pattern occurs. *Pinus edulis* Engelm. and *Juniperus* spp. become the dominant features in the vegetation. In one canyon near Bat Cave several trees of *Pinus ponderosa* Dougl. ex P. Laws. occur, while, in some protected areas of this piñon-juniper belt, trees of various species of Quercus are found.

Vegetation in the Past. The species identified among the vegetal remains found in Bat Cave would seem to indicate that the natural vegetation which occurs today is not substantially different, except in a few character-

istics, from that of the past. The region is not one where such plants as maize, beans and squashes, none of them species notable for drought resistance, would be expected to occur in the wild, and certainly at the present time conditions are scarcely suitable for their cultivation. At an earlier period, however, when Lake San Augustin was a permanent body of water with a water level considerably higher than the present level of the plain, maize, beans and squashes could have been, and undoubtedly were, grown on its shores.

Description of the Site. Bat Cave is situated on the eastern edge of the Plains of San Augustin about 165 feet above the level of the lake floor and at an altitude of about 7000 feet. Carved out of an almost vertical cliff, apparently by wave action, Bat Cave is actually a series of six more or less separate caves. The largest of these is about 100 feet deep and 75 feet from floor to roof. A second is approximately 40 feet deep and 30 feet from floor to roof. Four smaller caves lying between these two are 10 to 20 feet deep and 10 to 15 feet high. It is from these smaller caves that the material described in this paper was excavated.

Excavation of Material. The refuse was removed in successive strata each about twelve inches in thickness. The lowest stratum which contained plant remains is designated as I and the uppermost as VI.

The bulk of the material was carefully excavated *in situ* by hand trowelling on a vertical face. The depth of the specimen was carefully noted in all cases. All the botanical material was packaged in separate lots for each area in the excavation.

The total depth of the deposits in which maize was found averaged between five and six feet. The entire

deposit bore artifacts without hiatus to the bottom where it rested upon a layer of water-washed gravel.

Dating. Dr. Ernst Antevs, who is preparing a separate report on the geology of Bat Cave and the surrounding region, estimates that the cultural deposits containing the maize had their beginning not later than 2500 B.C. This estimate is based on the fact that the refuse rests upon a layer of windblown sand and dust which represents a period decidedly drier than the present. Antevs believes the sand and dust were deposited between 5500 B.C. and 2500 B.C. The level representing this very dry age rests upon old beach gravels which were laid down during a preceding pluvial period. The gravel rests on bedrock. The top level of the maize-bearing deposit is dated by pottery as 500 A.D. to 1000 A.D. Thus, the deposit containing maize covers a span of not less than 3000 years. Exact dating of the site is not, for our purpose, of overwhelming importance. Much more significant is the fact that the characteristics of the maize from Bat Cave are such as to make it the most primitive which has so far been discovered; and, even with conservative dating, it is the most ancient.

Maize Remains. The maize remains isolated from the refuse comprised a total of 766 specimens of shelled cobs, 125 loose kernels, eight specimens of husks, ten of leaf sheaths, and five of tassels and tassel fragments. Most of the specimens, even those from the lowest stratum, were extraordinarily well-preserved, with the long plant hairs on the epidermis of the glumes and the surface of the cupules still intact. Indeed, most of the vegetal material is in such an excellent state of preservation that botanists would be inclined to question the geologists' estimates of its antiquity did not the specimens of maize from the different strata exhibit a distinct evolutionary sequence.

Shelled cobs comprised by far the largest fraction of the maize remains found in Bat Cave. These included 52 separate lots, totaling, as has already been stated, 766 specimens. Of these, 471 were sufficiently well-preserved to be studied for a number of distinct botanical characteristics.

Our method of studying the prehistoric cobs was to snap each cob in two, examining the two surfaces thus exposed under a dissecting microscope. The number of characteristics which can be studied in the maize cob is truly astonishing. Those which we considered are listed in Table I. Further studies of the maize cob will undoubtedly reveal other characteristics which can be utilized in comparing maize populations. Lenz (1948), for example, describes a "rachis flap" which is prominent in some varieties and relatively inconspicuous in others. The rachis flap was so erratically distributed in the Bat Cave specimens that we gave no serious attention to it. Nor did we attempt to measure rachilla length, another characteristic in which maize varieties differ considerably, according to Lenz (1948) and Cutler and Cutler (1948). However, some of the other characteristics which we did investigate, such as length and shape of the glumes, are strongly correlated with rachilla length, so that indirectly we undoubtedly took this character into account.

The characteristics in which the specimens from the six strata are compared are described below.

Length of Cob. This is a simple measurement made on all cobs which were intact with respect to length or so nearly intact that their original length could be estimated. The data in Table I show that there is little difference in the mean length of the cobs in the first three strata. Thereafter, there is a more or less progressive in-

TABLE I. CHARACTERISTICS OF THE PREHISTORIC MAIZE OF BAT CAVE COMPARED BY STRATA

Characteristics	Stratum I	II	III	IV	V	VI
No. of separate lots	2	4	8	6	8	24
Total No. of cobs	25	55	77	146	118	345
No. cobs scored	19	23	38	75	78	238
No. cobs intact in length	4	2	5	13	17	25
Length intact cobs—cm. max.	9.5	10.3	9.5	13.8	15	16.5
" " " " min.	6	7.2	6.5	5.1	5	4
" " " " mean	7.3	8.4	7.7	8.5	9.6	9.3
Mean diameter of rachis mm.	7.5	8.6	7.9	8.4	9.9	11.2
" " " cob "	14.8	15.7	15.3	16.2	17	17.5
Index cob/rachis—max.	2.5	3	2.8	2.6	2.5	2.8
" " " min.	1.6[*]	1.5	1.4	1.2	1.2	1.2
" " " mean	1.9	1.8	1.9	1.9	1.7	1.6
Rows of grain—max.	14	16	16	20	16	20
" " " min.	8	8	8	4	8	4
" " " mean	10.7	12	11.2	12	11.6	11.4
Rachis tissue % spongy	28	88	58	43	29	38
" " " horny	72	12	39	39	28	24
" " " bony			3	18	43	38
Surface of cupules % glabrous	19	4	8	8	8	22
" " " " hispid			3	13	25	15
" " " " hirsute	81	96	89	79	67	63
Lower Glumes Texture % fleshy	97	91	71	56	25	40
" horny	3	9	26	36	18	21
" bony			3	8	57	39
Surface " glabrous	100	96	95	79	92	85
" hairy		4	5	21	8	15
Venation " slight	10	44	18	51	6	16
" none	90	56	82	49	94	84
Upper Glumes Shape % boat	20	13	16	12	7	8
" intermed.	80	61	47	59	38	49
" collar		26	37	29	55	43
Texture " chaffy	100	48	47	61	37	49
" fleshy		52	53	39	59	48
" horny					4	3
Surface " glabrous	100	96	89	71	74	78
" hispid			3	8	3	3
" hairy		4	8	21	23	19
Venation " strong	30	30	29	56	21	26
" intermed.	53	26	55	28	41	43
" none	17	44	16	16	38	31
Tunicate alleles % tu					1	
" " " tu^w			8	1	33	55
" " " tu^f	80	92	82	73	61	42
" " " tu^h	20	8	10	26	5	3
Teosinte introgression % none	100[*]	100[‡]	73	43	9	27
" " % intermed.			22	52	58	61
" " % strong			5	5	33	12
Kernels Total No.	2	2	10	20	67	24
Av. length 1/1000 in.	275	293	280	312	302	316
Av. thickness " "	193	247	223	210	236	217
Width max. 1/1000 in.	258	301	340	376	398	428
" min. " "	230	229	213	214	197	201
" mean " "	244	265	265	284	308	333

[*] There is one cob with a cob/rachis index of 1.2 which also shows evidence of strong introgression of teosinte. Since this cob is atypical of the stratum in other characteristics as well it is undoubtedly an intrusion and is not included in this datum.

[‡] There is one cob in this stratum which shows unmistakable teosinte introgression but which is atypical in other respects and is probably an intrusion.

crease in mean length from stratum to stratum. Even more interesting than the mean length of the cob is a comparison of the maximum and minimum lengths. Beginning with the fourth stratum there is a progressively greater divergence between the shortest and the longest ears in each stratum. Part of the increase in range of variation may be attributed to a progressive increase in the size of the samples available, but there is no doubt that there is a true increase in the range of variation beyond that resulting from sampling. This is reflected not only in the size of the cob but in many other characters as well.

Diameter of the Rachis and Cob. When a cob of maize is snapped in two it is quite easy, in examining the cross section, especially of the lower half, to distinguish between an inner zone made up of the rachis and an outer zone made up of the glumes. These zones represent two concentric circles whose diameter is easily determined with a pair of calipers. The data in Table I reveal that there are no significant differences in the diameters of the rachis and the entire cob in the three lowest strata. Thereafter, however, there is a progressive increase in mean diameter of the rachis and in mean diameter of the entire cob from stratum to stratum.

The Cob/Rachis Index. Much more impo1 .nt than the actual diameter of these two concentric circles representing the rachis and the entire cob is the ratio of one to the other. This ratio, called the cob/rachis index and obtained by dividing the larger figure by the smaller, may prove to be one of the most useful measurements yet employed in studying and classifying maize varieties, for it has a clear-cut and definite genetic basis involving changes in alleles at the *Tu-tu* locus on the fourth chromosome. The existence of four alleles—tunicate (*Tu*),

half-tunicate (tu^h), weak-tunicate (tu^w), and non-tunicate (tu)—at this locus has already been demonstrated (Mangelsdorf, 1948). In addition, a condition intermediate between weak-tunicate and half-tunicate is found in some races of maize including the Chapalote maize of Mexico. Since this form of tunicate, which has not yet been studied genetically, produces approximately the same effect when homozygous as does half-tunicate when heterozygous, it may appropriately be called fourth-tunicate and tentatively given the symbols tu^f, subject to verification by later genetic tests.

The importance of these *Tu* alleles in connection with our present studies lies in the fact that a change from a higher to a lower allele in the series is almost invariably accompanied by a drastic change in the cob/rachis ratio. In other words, when the glumes become shorter, the rachis, other factors remaining constant, automatically becomes thicker. This is easily demonstrated in modern isogenic stocks which are segregating for two alleles in the *Tu* series. A comparison of three such stocks is shown below:

Stock	*Cob/Rachis Index*
Inbred A158 tu^htu^h	2.9
" " tu^htu	2.1
" " $tutu$	1.5

The cob/rachis index, therefore, is in substantial part a simple estimate of the degree to which a variety of maize has departed from a primitive tunicate form toward the modern non-tunicate condition. It must be realized, however, that in addition to changes in both the diameter of the rachis and that of the entire cob resulting from changes in *Tu* alleles, there are other differences resulting from the action of a vast number of modifying factors.

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It is interesting to note that the cob/rachis index in the Bat Cave maize varies from 3.0, a condition in which the rachis is slender and the glumes are prominent, to 1.2, a condition in which the rachis is large and the glumes are relatively short. The cob/rachis index is, however, relatively constant through the three lower strata, but shows some change in the upper three. It is of particular interest to note that, although new types with a low cob/rachis index appear in the upper strata, the original types with a high index, though becoming somewhat less frequent, do not disappear. If human selection had been operating in favor of the lower alleles at the *Tu-tu* locus, it certainly had not, in the period represented by the uppermost strata, succeeded in completely eliminating the higher alleles. There has, as in other characteristics, been primarily an increase in the range of variation.

Rows of Grain. There has been no constant change in the number of rows of grain from stratum to stratum. An increase in the circumference of the cob should result either in an increased number of rows of grain or in wider grains. It will be shown later that there has been a progressive increase from stratum to stratum in the average width of the grains. Similarly, although it is not clearly revealed by the summarized data, there has been an increase in the number of rows as a consequence of the increase in the circumference of the rachis. Indeed, the principal variation in the two lower strata has been concerned largely with the diameter of the rachis, the prominence of the glumes and the number of rows. Of 41 ears which were scored for both row numbers and *Tu* allele, 16 were classified as fourth-tunicate, 8 as half-tunicate and 17 as intermediate between these two conditions. The average row numbers of these three groups is shown below.

Type of Ear	Average Row Number
Half-tunicate	10.5
Intermediate	11.2
Fourth-tunicate	11.9

Here, then, is another factor not previously recognized which is involved in the complex problem of row number in maize. It can now be said that, other things being equal, the lower the allele of *Tu*, the higher will be the number of rows on the ear.

Rachis Tissue. It is a common observation both of practical farmers and students of maize that there is a great variation in the hardness or stiffness of individual cobs. Lenz (1948) has recently reported that the texture of the cob depends to a large extent upon the relative amount of heavily schlerenchymatized tissue. A histological examination of the nearly 500 cobs included in this study was out of the question, but it was possible to score the cobs with respect to the tissue of the rachis by testing with a dissecting needle the surface exposed when the cob was broken. The tissue immediately below the epidermis of the rachis was used for this purpose; the cobs were classified as having spongy, horny or bony tissue. Bony cobs, such as would be expected from an introgression of Tripsacum or teosinte, do not make their first appearance until Stratum III where they occur to the extent of three percent. The percentage of bony cobs reaches a maximum of 43 percent in Stratum V and falls off slightly to 38 percent in Stratum VI.

Surface of Cupules. The alveoli or cupules in the rachis from which the paired spikelets arise vary considerably in the nature of their surfaces. Some are virtually glabrous, others are beset with short stiff hairs (hispid) and still others are lined with long slender hairs (hirsute). Glabrous and hirsute types occur in all strata, but cupules

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with hispid surfaces do not make their appearance until Stratum III. Thereafter, they increase progressively to Stratum V and fall off again in VI, a pattern quite similar to that exhibited by bony cobs and probably for the same reason. A strong introgression of teosinte into maize, as in some segregates from maize-teosinte hybrids, results in glabrous cupules. This is not surprising, since the inner surface of the bony shell of teosinte, the counterpart of the cupule in the rachis of maize, is always glabrous. But a smaller amount of teosinte introgression may cause the hairs in the cupule merely to be shorter and stiffer. Thus the hispid condition encountered in later strata of the Bat Cave material may well be a manifestation of teosinte (or Tripsacum) introgression.

Lower Glumes. The lower glumes of an ear of maize vary: (a) in texture which may be chaffy, fleshy, horny or bony; (b) in surface which may be glabrous, hispid or hairy; and (c) in venation which may be apparent to the eye or obscured by the thickness of the tissues. The data in Table I reveal that there are no truly chaffy or membranaceous glumes such as are found in modern pod corn. Neither are there bony glumes such as those found in teosinte until we reach Stratum III. Thereafter, the percentage of bony glumes increases progressively to Stratum V and falls off slightly in Stratum VI. The induration of the glumes is almost a certain sign of teosinte or Tripsacum introgression. Types with bony glumes similar to those found in the upper strata of this material are readily synthesized experimentally by substituting one or more chromosomes from teosinte for the corresponding maize chromosome. There is little doubt that the strong, bony glumes evident in much of the Bat Cave material is the product of introgression from teosinte or

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Tripsacum. The significant fact is that this introgression is not apparent in the lower strata.

The fact that all glumes in the lowest stratum are glabrous may be of some significance. Cutler and Cutler (1948) report that hairs on the pistillate glumes are occasionally present in numbers proportional to those found on the leaf sheath. Insofar as glabrous pistillate glumes are associated with glabrous leaf sheaths, we may infer that the early Bat Cave corn was glabrous. Completely glabrous husks, found in Stratum II and described later, support this conclusion.

The venation of the lower glume may be obscured because the glume is fleshy or because it is indurated as in teosinte. Both conditions are encountered in this material. Glumes on 90 percent of the ears in the lowest stratum show no venation because they are fleshy. In Stratum VI, however, the lack of venation occurs on both fleshy and indurated glumes.

Upper Glumes. The upper pistillate glumes, easily studied on the exposed end of the lower half of a broken cob, possess several interesting characteristics. They vary in shape from those which resemble one end of a boat and have obviously once enclosed a kernel, to a short, stiff half-collar which once surrounded the base of a kernel. Forms intermediate between these two extremes are common. Boat-shaped upper glumes characteristic of true pod corn are found in all six strata, but are most common in Stratum I. Collar-shaped glumes are most common in Stratum V.

The upper glume is most commonly membranaceous or chaffy, but may be fleshy, and, as in teosinte and Tripsacum, even horny. All of the ears in the lowest stratum have chaffy upper glumes. Horny upper glumes occur only in Strata V and VI.

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The surface of the upper glumes, like that of the lower, may be glabrous, hispid, or hairy, although the two glumes are not necessarily identical with respect to these characteristics. Only glabrous upper glumes were found in Stratum I and glabrous glumes continued to predominate throughout all strata. Hairy upper glumes made their first appearance in Stratum II and increased in frequency in successive strata up to V. Hispid upper glumes first appeared in III and occurred in small percentages in the remaining strata.

The visible venation of the upper glume is strongly but not completely correlated with its shape and texture. The data on venation of the upper glume in this material are generally in agreement with the data on shape and texture. Strongly veined glumes, like those which are boat-shaped or chaffy, have their lowest frequency in Stratum V.

Tunicate Alleles. An attempt was made to classify the cobs with respect to the degree to which they were tunicate or non-tunicate. As has already been mentioned, four degrees of tunicate—Tu, tu^h, tu^w, and tu—are known and a fifth, tu^f, intermediate between tu^h and tu^w, is believed to occur.

No cobs with glumes as strongly developed as those of modern pod corn of the genotype $Tutu$ were found, but true pod corn of the half-tunicate type occurred in each of the six strata. Pod corn of the fourth-tunicate type also occurred in all strata and indeed was the most common type in all except the uppermost. Weak-tunicate first appeared in Stratum III and became the most common type in VI. Only one ear regarded as non-tunicate was encountered.

These data indicate strongly that one of the principal factors involved in the evolution of maize has been a

gradual replacement of the higher alleles in the *Tu-tu* series by the lower. Mangelsdorf (1948) has shown that both *Tu* and *tu^h* have relatively high mutation rates. It is evident from the Bat Cave material that mutations at the *Tu-tu* locus have occurred and that there has been a gradual decline in the frequency of the higher alleles and an increase in the frequency of the lower. This, in turn, has had far-reaching effects upon the size of the rachis, on the size of the entire cob, on the space available for the vascular system, upon the length of the rachillae which bear the kernels and undoubtedly upon the ultimate yield of grain. The importance of the changes in relative frequency of the different *Tu* alleles can scarcely be over-emphasized.

Teosinte Introgression. The hypothesis of Mangelsdorf and Reeves (1939) with respect to the origin of maize postulates that teosinte is the product of a natural hybridization of maize and Tripsacum which was followed by an introgression of teosinte (or Tripsacum) germplasm into maize. The origin of teosinte as the progeny of maize and Tripsacum has not yet been finally proved, although much additional evidence in support of the hypothesis has been accumulated since 1939 (cf. Mangelsdorf, 1946). For the purpose of this paper, however, it is not necessary to debate the question of the origin of teosinte. We are here concerned primarily with the question whether there is evidence of such an introgression of teosinte into maize. The answer is that there is strong evidence of such introgression, but only in the later strata of the Bat Cave material.

The scores for teosinte introgression represent estimates involving personal judgment which in turn is based upon an extensive experience in studying derivatives of maize-teosinte hybrids produced experimentally. When

a cob has bony rachis tissue, bony lower glumes, upper glumes lacking in venation and a hispid cupule, it is almost certainly a product of teosinte introgression. If it has some of these characteristics, but not all, it is assumed to represent teosinte introgression of a lower order.

In each of the first two strata there was only one cob which showed evidence of strong introgression of teosinte. These cobs were atypical of the strata in almost all of their characteristics and are probably "intrusions," a convenient term employed by archaeologists to describe specimens which are found in any part of a cultural deposit in which they obviously do not belong. With rats and other rodents digging burrows in ancient refuse heaps, it is almost inevitable that a specimen from a higher stratum will occasionally find its way into a lower. Intrusions, therefore, have a real basis in fact and are not merely a device for conveniently explaining exceptions.

Cobs showing evidence of teosinte introgression occur in somewhat greater frequency in Stratum III, but are not common. These, too, may be intrusions or they may result from the fact that the line of demarcation between the strata is entirely arbitrary. In any case, not until Stratum IV is reached can we be certain that teosinte-contaminated maize has become a conspicuous part of the population.

The amount of teosinte introgression is greatest in Stratum V and drops off perceptibly in Stratum VI. Two possible reasons for this decline come to mind at once. The first is that introductions of non-tripsacoid maize from other regions have "diluted" the teosinte germplasm; the second is that some of the more obvious effects of teosinte have become modified through the development of an appropriate modifier complex. Since there is no clear-cut evidence of an introduction of non-tripsacoid maize on a large scale, the second possibility

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appears to be the more plausible one. The senior author (1946) suggested several years ago that much of the recent evolution in maize has been a matter of absorbing the morphological assets of teosinte while suppressing its morphological liabilities through selection for appropriate modifier factors. The material from Bat Cave is almost direct evidence in support of this thesis.

The interaction between the various alleles of *Tu* and the introgression of teosinte germplasm is an interesting one which is clearly revealed by some of the cobs in Strata IV and V. In a recent paper (1948) the senior author illustrated a spike of tunicate teosinte produced by introducing the *Tu* gene into teosinte through repeated back-crossing. The rachis was reduced to a slender disarticulating stem. The prominent glumes, quite distinct from the bony glumes of teosinte in size and structure, had, nevertheless, taken on a coriaceous quality very different from the papery or chaffy glumes of pod corn. They seemed almost to be a product of distributing over a large volume of tissue all of the factors for hardness and stiffness ordinarily found in a small volume.

Teosinte introgression has similar effects upon genotypes representing lower alleles in the *Tu-tu* series. Plate XXVI, Figs. F, G, H, illustrates three cobs from Bat Cave which are similar, if not identical, with respect to their alleles of *Tu*, but which differ decidedly in the amount of teosinte introgression.

Evidence for introgression of teosinte germplasm into maize was not confined to a general increase in the hardness of the rachis and outer glumes, since individual characteristics of teosinte also made their appearance. Three cobs were found with the distichous arrangement characteristic of teosinte. These occurred in Strata IV, V, and VI. Two cobs were found which bore single spikelets, also a teosinte characteristic. These occurred in Strata

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IV and V. All of the evidence combined points to two conclusions with respect to the rôle of teosinte in the origin and evolution of maize: (1) Maize did not originate from teosinte; (2) The course of evolution of maize in its later stages has been strongly affected by an introgression of teosinte germplasm. If it should ever be established beyond a reasonable doubt that teosinte is a hybrid of maize and Tripsacum, then a third important conclusion would be possible; namely that the hybridization between maize and Tripsacum which produced teosinte must have occurred not later than 500 B.C. and perhaps considerably earlier.

Evolution of Kernel Size

The primitive people who grew the maize whose remains were found in Bat Cave were evidently extremely efficient in their corn-shelling operations. Not a single cob among the 766 recovered from the digging bore even one normal kernel. However, a total of 125 loose kernels, all reasonably well-preserved, were uncovered in the refuse and some of these were found in each of the six layers. The kernels in each of the two lower strata are small and corneous, and were undoubtedly capable of popping. Thus, the primitive maize of Bat Cave was, as Sturtevant (1894) supposed primitive corn to be, both a *pod* corn and a *pop* corn.

The kernels, like the cobs, show a progressive increase in mean size from stratum to stratum. They were measured in three dimensions and, since the calipers used registered in thousandths of an inch, these units were also used in computing the mean as well as the maximum and minimum dimensions which are set forth in Table I.

It is apparent from the data in Table I that, while there is little change in the mean thickness of the kernels from stratum to stratum, there is a noticeable if somewhat

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irregular increase in mean length and a marked and progressive increase in average width. Since kernel width has increased proportionately more than length, it furnishes the most useful dimension for detailed study.

Even more striking than the increase in average kernel width is the progressive increase in the maximum width (width of widest kernel) from stratum to stratum. This increase is virtually linear, but the linearity is probably spurious, since it is scarcely to be believed that the several strata represent identical periods of time, or that genetic changes of a given order always produce the same change in absolute dimensions whether acting upon small or large kernels. Furthermore, part of the increase in maximum size is nothing more than a consequence of increasing the size of the sample. This factor, however, does not account for all of the increase in maximum size, since there is a substantial increase from Stratum IV to Stratum VI, although the samples from the two strata are approximately equal in size. Furthermore, the cobs, even though they lack kernels, furnish indirect evidence of a progressive increase from stratum to stratum in the mean and maximum width of the kernel.

Although there is a progressive increase in kernel width from stratum to stratum, the smaller-kerneled types with which the series began did not disappear from the scene when the new types with larger kernels came into existence. What has actually occurred is that there has been an appreciable increase in the range of variation with respect to kernel size. This is illustrated by Plate XXIV, Fig. A.

The marked increase in variation in kernel size in a relatively short period of time provides some indication of the way in which variability accumulates in a man-made environment in which the pressure of natural selection has been reduced or released. Here, perhaps, is the

key to the enormous diversity found in so many species of cultivated plants and domestic animals. Here, too, perhaps, is a clue to the rapidity with which organisms, in nature, can evolve in the face of drastic changes in the environment.

Evolution of the Husks

Although only eight specimens of husks were found in the Bat Cave remains, these differ sufficiently in their characteristics from stratum to stratum to allow some far-reaching inferences to be drawn with respect to the nature of the primitive maize inflorescence and the evolution of husks during domestication.

No specimens of husks were found in the lowest stratum. Only one specimen was found in Stratum II, but this single specimen, although it represents the husk covering of less than half of the ear, has an extremely important story to tell.

The husk appears to be intact with respect to length and reaches a maximum length of 24.5 cm. Four leaf sheaths are included, and the number may tell something of the relative height at which the ear arose. If primitive maize resembled either of the maize relatives, teosinte or Tripsacum, its lateral branches would have had a node number approximately equal to the node number on the primary stalk above the point of origin of the branch. This allows us to infer that the ear was borne at the fifth node below the tassel, but it tells us nothing about the number of nodes which might have occurred below the ear.

All husks have prominent parallel veins widely spaced. There is no anastomosing venation. It is primitive, undifferentiated husks of this type which produce the "striations" on the surface of the kernels in ears which are tightly enclosed in husks (Anderson 1944a). Striated ker-

nels may therefore be regarded as a primitive character.

Perhaps the most important characteristic of this husk is that it shows no evidence of ever having been shaped around an ear. Furthermore, the stem or shank on which it occurs is quite slender, so slender indeed that, of the cobs which occur in Strata I and II, only a cob similar to that illustrated in Plate XXVII could have been borne on it. The husks, as shown in this Plate, are far longer than needed to enclose an ear of this type.

All of these facts combined point to the almost inescapable conclusion that the husks at this stage in the evolution of maize did not enclose the ear. Instead, they were nothing more than an involucre of leaf sheaths, not greatly modified, subtending and surrounding the base of the pistillate inflorescence, but by no means completely enclosing it.

The remaining seven specimens of husks together are not as interesting as the single specimen found in Stratum II. One of the specimens found in Stratum V appears to be intact or almost so and has a maximum length of 10.5 cm. It includes five leaf sheaths, all glabrous and lacking in leaf blades and ligules. The veins are parallel, but are more closely spaced than in the sheaths found in Stratum II. The husks in Stratum V differ from those in Stratum II primarily in their shape, which gives definite evidence of having once enclosed an ear.

Two other specimens found in Stratum V differ from the one described immediately above in having scattered hairs and numerous prickles on the outer sheaths and anastomosing venation on the inner. Both show evidence of having once enclosed an ear.

The four specimens found in Stratum VI are too fragmentary to be of great value. Two of the specimens, however, show evidence of having once been shaped around an ear. Two of the four specimens are glabrous.

The third has its inner surface beset with short prickles while the outer bears scattered hairs and prickles. The last specimen bears numerous short hairs on the inner surface and between the veins on the outer surface. The veins themselves bear longer and more numerous hairs on the outer surface. Only parallel venation was found on three of the four fragments; anastomosing venation was apparent on the fourth.

Cutler (1946) has pointed out that the husks of maize are not fundamentally different from a variety of similar structures found in other genera of grasses, and he compares them specifically with a kind of fasciation sometimes occurring in the genus Trichachne in which the lateral inflorescence is enclosed by the leaves of the culm on which it is borne. The husks found in Stratum II of the Bat Cave remains would indicate that Cutler's comparison is valid. Furthermore, the later evolution of the husk covering is quite consistent with the modification of leaf sheaths which occur in other grasses.

The leaf sheaths which comprise the husks obviously became wider during the evolution of maize and eventually completely enclosed the ear. The leaf blade and ligule were lost. The outer and inner sheaths became differentiated, the latter becoming thin and papery with anastomosing venation and were no longer capable of producing striations on the kernels. These changes are quite in keeping with the morphological pattern in other genera of grasses. Arber (1934), speaking of modification of leaf sheaths in the grasses, makes the following statement:

"An exaggeration of the size [width] of the leaf-sheath, and a corresponding reduction in the limb, occur as part of the normal development in the uppermost foliage leaf enclosing the inflorescence in many grasses, such as *Phalaris canariensis* L. and *Alopecurus pratensis* L. In the xerophytic South African grass, *Ehrharta aphylla* Schrad., this type of change has gone so far that the lamina is reduced to a mere point." [1]

[1] Reference to figures omitted in this quotation.

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The figures that accompany Arber's statement are particularly interesting in illustrating the marked broadening of the sheath in *Phalaris canariensis* and the reduction of the leaf blade to a mere point in *Ehrharta*.

Arber also describes and illustrates a broadening and shortening of the leaf sheaths and a reduction in the laminae in *Agropyron repens* Beauv., resulting from injury by insects. And Hitchcock (1935) illustrates a number of species of grasses in which the sheath or sheaths immediately below the inflorescence have become shorter and broader and have largely lost their laminae. It is evident, therefore, that the development of the husks in maize is nothing more than an exaggerated form of a morphological development which is widely distributed in the Gramineae.

In several recent papers (1946, 1948) the senior author described the evolutionary steps which were thought to have occurred in maize during evolution under domestication. In the light of the direct evidence now bearing on this point the views previously expressed are subject to possible modification. For example, it was assumed that wild maize bore mixed staminate and pistillate inflorescences terminally on lateral branches whose sheaths and laminae were essentially identical with those on the main stalk. Although this assumption has not yet been shown to be erroneous, another possibility is now apparent. It is quite possible that wild maize already had distinct staminate and pistillate inflorescences, and that a shortening of the internodes immediately below the pistillate inflorescence had already occurred, giving rise to an involucre of leaf sheaths which surrounded the base of the ear but did not enclose it. There is no reason why a plant with such an inflorescence could not have existed in a wild state. There is, at least, no doubt that such a plant did exist in the early stages of domestication.

One more important and clear-cut conclusion can be drawn from the evidence furnished by the prehistoric husks. Had maize originated from teosinte, as some botanists still suppose, then the early primitive races of maize, only slightly removed from teosinte in their characteristics, might be expected to possess short husks scarcely covering the ears. The early evolution of the husks would then have become a matter of a progressive increase in length to enable the husks to enclose progressively longer ears. In the Bat Cave material the evolutionary sequence in the husks is exactly the reverse of this. The earliest husks are the longest. Indeed, they are several times longer than the longest ear in the same stratum. The early evolution of husks has been a matter of their becoming shorter and wider rather than longer.

Thus, the accumulated circumstantial evidence against the hypothesis that maize originated from teosinte is finally reinforced by direct evidence which is almost conclusive.

Leaf Sheaths

In addition to the husks which are largely modified leaf sheaths, ten specimens of true leaf sheaths were found—one from Stratum IV, the remaining nine from VI. The specimen from Stratum IV is completely glabrous; of the nine specimens from VI, four are completely glabrous on both inner and outer surfaces, three have hairs and prickles on both surfaces, one is glabrous on the outer surface and beset with numerous short hairs on the inner, and one bears short hairs on the outer surface but is glabrous on the inner.

The significance of these variations is not yet clear. Only one fact is certain. At least part of the maize found in Bat Cave possessed glabrous leaf sheaths. True glabrousness is not common in maize varieties today, except

among those grown at high altitudes in Ecuador, Peru and Bolivia, although it is occasionally encountered in Guatemala[1] and Mexico. The inheritance of glabrousness (unpublished data) does not appear to be particularly complex and it is possible that the characteristic has appeared more than once in the evolution of maize under domestication. On the other hand, the fact that there is a large center of glabrous maize at high altitudes in South America may not be without significance in connection with a consideration of the early glabrous maize from Bat Cave which also grew at a relatively high altitude.

TASSELS

Anderson and his co-workers (1942, 1944b, 1948) have repeatedly emphasized the importance of studying the maize tassel as a means of understanding the morphology of the ear, and in studying the tassel they have discovered an array of characteristics which promise to be invaluable in the classification of living maize varieties. Tassels, however, are by no means as enduring as ears and cobs, nor are they so likely to be collected in great numbers by primitive peoples or deposited by them in refuse heaps or graves. Only five specimens of tassels were found in the Bat Cave remains, one in Stratum III, three in IV and one in V.

The specimen in Stratum III consisted of a fragment of a lateral tassel branch. This included five nodes, of which three each bore an extra spikelet. This condition, first described by Cutler (1946) and called "multiplication," is common in the maize varieties of South America.

[1] Mangelsdorf and Cameron (1942) described as glabrous many varieties from Guatemala. This is an error in terminology. Most of the varieties described by them as glabrous, although lacking the prominent hairiness so characteristic of high-altitude varieties of Mexico and Central America, are actually hispid.

It is superficially similar to, but actually quite different from, a condition which Anderson (1944b) has designated as "condensation," in which there is a telescoping of internodes to the extent that two or more pairs of spikelets *appear* to arise at the same node. Condensation is common in the maize of Mexico and Central America.

The spikelets on the single specimen from Stratum III had their glumes sparsely covered with prickles.

The three specimens from Stratum IV comprised two fragments and one intact tassel. The first, a fragment of a central spike, had its glumes covered with short hairs and prickles and showed neither condensation nor multiplication. The second, a fragment of a branch, had its glumes sparsely covered with hairs and prickles and showed both multiplication and condensation. It included 12 nodes upon which were borne 37 spikelets, 13 more than should have occurred in the absence of both multiplication and condensation. One of the extra spikelets was the result of multiplication; the others, 6 pairs, were the consequence of condensation. The condensation ratio is, therefore, 1.5.

The intact tassel in this stratum comprised a lax central spike and three branches. Its glumes were covered with hairs and prickles, and the tassel showed neither multiplication nor condensation. It is the kind of tassel, which, among living varieties, is found only in early-maturing types.

The single specimen found in Stratum V had its glumes covered with long hairs. The fragment included 21 nodes and was free of both condensation and multiplication since there were no extra spikelets at any node.

No pistillate spikelets were found in any of the fragments or in the intact tassel.

So far as these few tassel specimens have any bearing upon the problem of evolution in maize, they suggest,

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but certainly do not prove, that (1) multiplication preceded condensation in this sequence, and (2) the maize grown by the Bat Cave people was early-maturing.

Primitive Maize Reconstructed

From a study of the cobs found in the lower strata of the Bat Cave material, supplemented by evidence supplied by fragments of husks, sheaths, and tassels, it is now possible to reconstruct a primitive maize with a substantial measure of confidence in the reliability of the reconstruction. The earliest Bat Cave material, which was probably an early-maturing race, had glabrous leaf sheaths. Its tassels bore lax central spikes and were sparsely branched. There was no condensation of the spikelets. Its ear, borne several nodes below the tassel, was surrounded, but not enclosed, by an involucre of slightly modified leaf sheaths (some bearing ligules and rudimentary laminae) which were at least twice as long as the ear itself. The small ear arising from the center of this involucre was a typical grass spike bearing paired pistillate spikelets on a slender rachis. The phyllotaxy was definitely spiral. Indeed, it was so strongly spiral that, in some cases, the cupule from which the spikelets arose was not at right angles to the vertical axis of the rachis but was more or less parallel to the sloping path of the spiral.[1] The lower glumes of the spikelets were fleshy, slightly flattened and lacking in conspicuous venation. They were quite similar to the glumes of sorghum and, like them, they did not completely enclose one half of the kernel. The upper glumes were somewhat longer than were the lower, a condition common among grasses, and were glabrous, chaffy, strongly veined, boat-shaped, and enclosed half of the kernel with length to spare. The

[1] In a previous paper the senior author (1945) expressed the opinion that spiral phyllotaxy in maize is largely the product of introgression from teosinte. He could scarcely have been more wrong.

kernels were small, slightly longer than wide, and corneous. This maize was both a pop corn and a pod corn.

An artist's reconstruction of this primitive maize, executed by Mr. Gordon W. Dillon to whom we are indebted not only for his artistry but also for his botanical acumen, is shown in Plate XXIV, Fig. B. In its phyllotaxy and the nature of its glumes the reconstruction is based upon an actual specimen from Stratum I illustrated in Plate XXIV, Fig. C. Since this specimen was not intact with respect to length, the reconstructed ear was drawn to correspond in length to an intact specimen in the same stratum. The size of the kernels in the reconstruction was determined by the shape of the upper glume which, as shown by examination under the microscope, had obviously partially enclosed a kernel. The kernels on the reconstructed ear are somewhat smaller than any which were actually found in Stratum II, but no smaller than several found in later strata.

It is possible that the kernels in primitive maize were not so completely enclosed by glumes as the artist's reconstruction would suggest and were actually more like kernels of varieties of grain sorghum which, although shorter than their glumes, are large enough to push the lower and upper glumes apart. In all other respects, however, Mr. Dillon's drawing represents an accurate and valid reconstruction of actual remains found in the lowest stratum of the Bat Cave material.

FACTORS INVOLVED IN THE EVOLUTION OF MAIZE

The evolutionary steps required to transform the primitive Bat Cave maize into a modern Corn-Belt Dent are no longer difficult to visualize. Indeed, many of them are clearly illustrated by the vegetal remains described in this paper. Elucidation of the remainder requires little more than a judicious use of the imagination.

The three principal factors in the evolution of maize have probably been: (1) a reduction in the pressure of natural selection; (2) a change in the alleles at the *Tu-tu* locus; (3) an introgression of teosinte germplasm into maize.

The principal effect of the first factor has been a tremendous increase in total variation. Variations, which in nature would have been rigidly selected against, survive and accumulate in a man-made environment where the struggle for existence is reduced to intra-specific competition. There is no evidence that human selection was an important factor in the early evolution of maize under domestication. Thus, in the absence of natural selection, and before human selection became a factor, the trend was one of creating a wider and wider range of variation.

The changes in the alleles at the *Tu-tu* locus have already been mentioned, but the full significance of these changes cannot be appreciated without considering the present-day products of this evolutionary trend. It has already been pointed out that changes from the higher to the lower alleles at the *Tu-tu* locus result in a reduction in the size of the glumes and an increase in the size of the rachis. These are the primary effects. The secondary effects, which are perhaps even more important, include a substantial increase in the vascular system of the ear, and a reduction in the length of the rachillae upon which the spikelets are borne. Cutler and Cutler (1948) state that the rachilla in teosinte, and in some species of Tripsacum, is compacted. They state further that in races of maize with long, slender rachillae the grains yield to pressure and can be pushed into the cob, while in races with compact rachillae the grains are firm.

All of these characteristics can easily be studied, with no more equipment than a pair of calipers and a rule, by an examination of the cross section of an ear exposed by

breaking the ear in two. It has already been mentioned that the cross section of a shelled cob comprises two concentric circles, the inner enclosing the zone of rachis tissue, and the outer the zone of glume tissue. The four upper diagrams in Plate XXVIII show cross sections of four cobs from Bat Cave and illustrate a sequence of changes in the cob/rachis index.

When the kernels are still attached to a cob, the cross section comprises three instead of two concentric circles, the diameter of the third circle representing the distance to the dorsal surface of the kernels. In true pod corn (*tuhtuh* and *Tutu* in Plate XXVIII) the third circle may lie within the second, but in all other types of maize it lies without. Now, if the average length of the kernels themselves is ascertained (for example, by measuring ten kernels laid end to end), the point at which the base of the kernels is attached to the rachillae is easily determined by measuring in from the third circle a distance equivalent to the average length of the kernel. These distances are shown by broken lines within the glume zone in the diagrams in Plate XXVIII. All of these are based upon actual diameters of the three concentric circles described above and, although fundamentally simple, are highly significant. They reveal, for example, that in the three genotypes *tuhtuh*, *tuhtu* and *tutu* from a relatively isogenic stock derived by repeated back-crossing to Inbred A158, there is a progressive increase in the diameter of the rachis, a progressive decrease in the size of the glume zone and a progressive shortening of the distance between the surface of the rachis and the base of the kernels. A similar comparison between *Tutu* and *tuhtu*, also in a relatively isogenic stock resulting from back-crossing to Inbred P39, illustrates a similar situation. In both of these series the changing relationship of rachis, glumes and kernels is entirely a matter of alleles at the *Tu-tu*

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locus. There is no doubt, however, that in nature teosinte introgression also has had its effects superimposed upon these. One of the most important of these effects is a toughening and hardening of the tissues of the glumes and rachis. Had this not occurred, the massive rachis and the short glumes of modern varieties could scarcely have come into existence.

The diagram of modern Dent corn (Plate XXVIII, fourth row) illustrates the lengths to which the evolutionary trends revealed by the Bat Cave cobs have now gone. The rachis has become massive and capable of enclosing an enormous vascular system. The glume zone has been reduced to a minimum, but the glumes have become more or less indurated. The distance between the surface of the rachis and the base of the kernels has been drastically shortened. The entire ear has become an extremely efficient grain-bearing structure, one which, to be sure, would scarcely be capable of surviving in the wild, but which in a man-made environment has no peer among cultivated cereals. Maize is, in many respects, the most efficient producer of foodstuffs among the cereals, and one of the factors in that efficiency is undoubtedly the nature of its pistillate inflorescence.

The Place of Origin of Maize

The evidence from Bat Cave sheds no new light upon the place of origin of maize as a wild plant. It seems scarcely possible that maize could have existed as a wild plant in the vicinity of Bat Cave since the present and past vegetation of this region is made up largely of xerophytic or near-xerophytic species. Furthermore, there is no more reason for suspecting that maize originated here than for believing that beans and squashes also had their origin in this region.

Mangelsdorf and Reeves (1939) concluded that maize

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had its origin as a wild pod corn in the lowlands of South America. The origin of maize from pod corn is well established by the Bat Cave remains, but this does not prove that maize originated in South America. The fact that weak alleles of pod corn still have their highest frequency in South America may be of some significance in this connection. Also significant may be the fact that the earliest Bat Cave maize is glabrous and that there is a center of glabrous maize in the highlands of Bolivia, Peru and Ecuador.

If an exact dating of the Bat Cave remains can be agreed upon, perhaps a correlation of the Bat Cave maize with prehistoric maize of the same period in South America will throw new light on the problem. In the meantime, the question of where maize originated as a wild plant is not answered by the new evidence.

SUMMARY

1. Remains of maize isolated from a cultural deposit in Bat Cave in New Mexico reveal a distinct evolutionary sequence.

2. The remains are conservatively estimated to represent a span of approximately 3000 years, beginning not later than 2500 B.C. They may actually have begun much earlier.

3. The maize excavated from the lower strata is the most primitive maize so far known. It is both a pod corn and a pop corn. The ear is not enclosed in husks, but is surrounded at its base by an involucre of leaf sheaths.

4. This early maize is clearly not derived from teosinte.

5. Beginning about midway in the sequence, there is strong evidence of an introgression of teosinte germplasm into maize.

6. There is a progressive increase in cob and kernel size from stratum to stratum.

7. Since ancient types did not disappear completely when new types came into existence, there is a progressive increase in total variability from stratum to stratum. This factor is believed to be of particular significance in the evolution of cultivated plants in general.

8. Changes in alleles at the *Tu-tu* locus and an introgression of teosinte are believed to be the two most important factors in the evolution of maize. These involve a progressive increase in the size of the rachis and the vascular system of the ear, a reduction in the size of the glumes, a shortening of the distance between the rachis and the base of the kernels and a hardening and stiffening of rachis and glume tissues.

9. The problem of where maize originated as a wild plant is not solved by the new evidence.

Acknowledgments

LITERATURE CITED

Anderson, Edgar. 1944a. Maíz reventador. Ann. Mo. Bot. Gard. 31: 301–314.

Anderson, Edgar. 1944b. Homologies of the ear and tassel in Zea Mays. Ann. Mo. Bot. Gard. 31: 325–342.

Anderson, Edgar and William L. Brown. 1948. A morphological analysis of row number in maize. Ann. Mo. Bot. Gard. 35: 323–336.

Anderson, Edgar and H. C. Cutler. 1942. Races of Zea Mays: I. Their recognition and classification. Ann. Mo. Bot. Gard. 29: 69–88.

Arber, Agnes. 1934. The Gramineae: A study of cereal, bamboo, and grass. Cambridge, England.

Brew, John Otis and E. B. Danson. 1948. The 1947 reconnaissance and the proposed Upper Gila expedition of the Peabody Museum of Harvard University. El Palachio 55: 211–222.

Cutler, H. C. 1946. Races of maize in South America. Bot. Mus. Leafl. Harv. Univ. 12: 257–291.

Cutler, H. C. and M. C. 1948. Studies on the structure of the maize plant. Ann. Mo. Bot. Gard. 35: 301–316.

Hitchcock, A. S. 1935. Manual of the grasses of the United States. U. S. Dept. of Agriculture Misc. Publ. No. 200.

Lenz, L. W. 1948. Comparative histology of the female inflorescence of Zea Mays L. Ann. Mo. Bot. Gard. 35: 353–376.

Mangelsdorf, P. C. 1945. Origin and nature of the ear of maize. Bot. Mus. Leafl. Harv. Univ. 12: 33–75.

Mangelsdorf, P. C. 1947. The origin and evolution of maize. In Advances in Genetics, Vol. I, pp. 161–207. New York.

Mangelsdorf, P. C. 1948. The rôle of pod corn in the origin and evolution of maize. Ann. Mo. Bot. Gard. 35: 377–406.

Mangelsdorf, P. C. and J. W. Cameron. 1942. Western Guatemala; a secondary center of origin of cultivated maize varieties. Bot. Mus. Leafl. Harv. Univ. 10: 217–252.

Mangelsdorf, P. C. and R. G. Reeves. 1939. The origin of Indian corn and its relatives. Texas Agr. Exper. Sta. Bull. 574.

Powers, William E. 1939. Basin and shore features of the extinct Lake San Augustin, New Mexico. Journ. Geomorphology 2: 345–356.

Sturtevant, E. L. 1894. Notes on maize. Bull. Torrey Bot. Club 21: 319–343, 503–523.

EXPLANATION OF THE ILLUSTRATIONS

Plate XXIII. The largest cobs, about two thirds natural size, found in each of the six successive strata in the Bat Cave material. Although there has been a progressive increase in maximum size from stratum to stratum, the type found in the first stratum has persisted throughout the series.

Plate XXIV. A. Variations in kernel size in the six successive strata of the Bat Cave material, natural size. The kernels, like the cobs, have increased in mean size from stratum to stratum, but the smallest size has persisted throughout the series. B. An artist's reconstruction, natural size, of the primitive pod-pop corn found in the lowest stratum of the Bat Cave refuse heap. This primitive maize shows no evidence of having been derived from teosinte. C. The cob from Stratum I, natural size, upon which the reconstruction in B is based.

Plate XXV. A. A cob, natural size, with prominent horny glumes produced experimentally from a maize-teosinte hybrid. The cob has been soaked in sulphuric acid to simulate aging. B, C, D, E and F are cobs from the upper strata of the Bat Cave showing teosinte introgression, natural size.

Plate XXVI. Bat Cave cobs, natural size, showing individual teosinte characteristics. A, B, C. Distichous spikes from Strata IV, V and VI, respectively. D, E. Cobs bearing some single spikelets, from Strata IV and V, respectively. F, G, H. Three cobs which are similar in their *Tu* alleles, but which differ in the degree of teosinte introgression.